# Spatial Capture-recapture with Partial Identity

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SUMMARY: I develop an inference framework for spatial capture-recapture data when two methods are used in which individuality cannot generally be reconciled between the two methods. A special case occurs in camera trapping when left-side (method 1) and right-side (method 2) photos are obtained but not simultaneously. I specify a spatially explicit capture-recapture model for the latent "perfect" data set which is conditioned on known identity of individuals between methods. The identity variable which associates individuals of the two data sets is regarded as an unknown in the model and I propose a Bayesian analysis strategy for the model in which the identity variable is updated using a Metropolis algorithm. The work extends previous efforts to deal with imperfect identity information by recognizing that there is information about individuality in the spatial juxtaposition of captures with encounter devices (traps). Thus, individual records obtained by both sampling methods that are in close proximity are more likely to be the same individual than individuals that are not in close proximity. The model proposed here formalizes the integration of spatial proximity information into models for the probabilistic determination of individuality using spatially explicit capture-recapture models.

KEY WORDS: animal abundance; animal sampling; camera trapping; capture-recapture; density estimation; DNA sampling; genotype error; latent multinomial; misclassification; noninvasive capture-recapture; partial information; population size; spatial capture-recapture models; spatially explicit capture-recapture.

## 1. Introduction

In this paper, I consider inference for capture-recapture models in which individual encounter histories are obtained by 2 types of sampling methods which may not be reconcilable. For example, by camera traps and DNA from hair snares (Fig. 1) or camera traps and scat surveys (Gopalaswamy et al. 2012a). Each method will, by itself, lead to individuality of the samples but the methods will not, in general, lead to the ability to reconcile individuals among themselves. A special case occurs when only camera trapping is used, but incomplete identity is obtained for some individuals, for example right or left flank only (McClintock et al. 2013; Bonner and Holmberg 2013). In camera trapping studies typically photos of both right and left sides of individuals are needed to produce individual identity (Karanth 1995, O'Connell et al. 2010). However, in practice, sometimes only a single side is photographed and traditional applications of capture-recapture based on camera trapping data have discarded these photos unless subsequent simultaneous photos were obtained. Camera trapping by itself can be thought of as a two method sampling problem with the methods being "left side camera trap" and "right side camera trap" while, in some cases, we might have records of both sides. A case of special importance is that in which there is a single camera at every site. In this case, *no* reconciliation to unique individuals is possible from the raw data. However, the potential to conduct camera trapping studies using only a single camera is extremely appealing due to the expense of equipment and the possibility of increasing the number of spatial sampling locations which is critical to spatial inference problems such as modeling resource selection (Royle et al. 2013) or landscape connectivity (Sutherland et al. 2015). Therefore maximizing the statistical efficiency of information from single trap studies is of substantial practical interest.

[Figure 1 about here.]

I propose a model for reconciliation of identity from multiple sample devices in which true identity is a latent variable. I provide an estimation framework using MCMC in which the individual identity of each encounter history is characterized by Monte Carlo sampling from the posterior distribution. The formulation of the model is facilitated by the observation that, conditional on the true identity, the model reduces to a basic spatial capture-recapture model for which MCMC can be implemented directly (Royle et al. 2009, Gopalaswamy et al. 2012b, Royle et al. 2014, ch. 17), but with a slightly distinct observation model accounting for multiple observation devices. The Metropolis-Hastings algorithm is used to update the latent identity variables.

McClintock et al. (2013) and Bonner and Holmberg (2013) considered precisely the same conceptual problem I consider here, using the latent multinomial model of Link et al (2010), but they considered classical *non-spatial* capture-recapture models. A key consideration in the problem of determining individuality is that there is direct information about individuality in the *spatial arrangement of captures*. For example, if nearby cameras capture photos of a right and left flank then those are more likely to belong to the same individual than if those photos were obtained by cameras far apart. So far this has not been accounted for in the previous work on misclassification in capture-recapture (Wright et al. 2009, Link et al. 2010, McClintock et al 2013, Bonner and Holmberg 2013; McClintock et al. 2014), although it has been recognized as being relevant in the combination of data from marked and unmarked individuals (Chandler and Royle 2013, Chandler and Clark 2014) and related mark-resight models (Sollmann et al 2013a; Sollmann et al 2013b). Therefore, in this paper I consider the unknown individuality in camera trapping or multi-method sampling in the context of spatially explicit capture-recapture models (Efford 2004; Borchers and Efford 2008; Royle et al. 2014). In addition to the formulation of the model as a spatially explicit model, so that information arising from spatial location of encounters can be integrated

into the determination of identity, the other element of this paper that deviates from most existing treatments of the latent multinomial model is the use of data augmentation (Royle et al. 2007, Royle and Dorazio 2012) to deal with unknown $N$. Using this formulation of the model yields a convenient treatment of the unknown population size parameter $N$ under which the observed data set is augmented to a maximum size of $M$ with all-zero encounter histories and the model is reformulated as a zero-inflated version of the known $N$ model. The parameter $N$ is replaced in the model by a set of data augmentation (zero-inflation) variables $z_i; i = 1, \ldots, M$. This is distinct from the treatments by Wright et al. (2009) who used reversible jump MCMC and Link et al. (2010) (and McClintock et al. 2013 and other applications) whose latent multinomial formulation can accommodate unknown $N$ by including the unobserved encounter frequency in the latent multinomial vector. However, that approach does not accommodate individual level effects, and spatial capture-recapture models as a class involve a latent individual variable $\mathbf{s}_i$ the activity or home range center of individual $i$. The one application of Link et al. (2010) using data augmentation to account for unknown $N$ is McClintock et al. (2014) who model individual heterogeneity. But their model was not spatially explicit and therefore does not use the spatial information to inform individuality.

The paper is organized as follows. In the following section I introduce multi-device observation models that potentially account for the dependent functioning of two sampling methods. In sec. 3 I define the 'ideal' data that arise under this observation model. That is, the data which are produced if individual identity were known across sampling methods. I also define the observable data and how the observable data are related to the ideal data. In sec. 4 I describe analysis of the model by posterior simulation using standard Markov chain Monte Carlo methods. I analyze a simulated data set in sec. 5 to explore the assignment of identity for a particular case. In sec. 6 I conduct a simulation study to evaluate the performance of

the Bayesian estimator of population size and encounter model parameters. Finally I discuss

extensions and the general relevance of the method in sec. 7.

## 2. Spatial encounter models

One of the key ideas developed in this paper is that information about individuality is

available from the spatial pattern of encounters. For example, two irreconcilable photos

are less likely to be the same individual as the distance between their encounter locations

increases and *vice versa*. Therefore, integrating a model that reconciles incomplete informa-

tion on individuality with spatial information about encounter location requires a modeling

framework that accommodates both types of information. Spatial capture-recapture models

(Borchers and Efford 2008; Royle et al. 2014) provide this framework.

In SCR models the probability of an individual being captured depends on both trap

location $\mathbf{x}$ and the spatial location of an individual's home range, embodied by the activity

or home range center $\mathbf{s}_i$ for each individual in the population $i = 1, 2, \ldots, N$. The activity

centers are regarded as a realization of a point process and treated in the model as a set

of latent variables (Borchers and Efford 2008, Royle and Young 2008). A typical model to

describe the encounter probability of individuals as a function of trap location and activity

center location is the hazard model having the form

$$p(\mathbf{s}, \mathbf{x}) = 1 - \exp(-h(\mathbf{s}, \mathbf{x}))$$

with, for example, $h(\mathbf{s}, \mathbf{x}) = p_0 \exp(-||\mathbf{s} - \mathbf{x}||^2/(2\sigma^2))$ where $p_0$ and $\sigma$ are parameters to be

estimated. Dozens of other models are possible, although cataloging them is not relevant to

anything here.

The activity centers $\mathbf{s}_i$ are not observable, but they are informed by the pattern of en-

counters (or non-encounters) of each individual. The customary assumption is that $\mathbf{s}_i \sim$

Uniform($\mathcal{S}$) where $\mathcal{S}$, the state-space of the random variables $\mathbf{s}$, is a region specified in the

vicinity of the traps. Typically the extent and configuration are not important as long as it is sufficiently large so that encounter probability is near 0 for individuals near the edge (e.g., see Royle et al. 2014, sec. 6.4.1). In the 'full likelihood' formulation of the model which is specified in terms of the population size parameter $N$, being the number of individuals inhabiting $\mathcal{S}$, population density is a derived parameter: $D = N/||\mathcal{S}||$.

Standard SCR models assume binary or frequency encounter events governed by the encounter probability model parameterized in terms of distance between trap and individual activity center. For multi-device models we require extending the ordinary encounter probability model to describe more complex encounter events. Two possibilities are discussed subsequently.

## 2.1 *Independent hazards model*

For two devices collocated at point $\mathbf{x}$ and that function independently it would make sense to assume an independent hazards model in which the probability of detection in device $m$ is:

$$p^m(\mathbf{s}, \mathbf{x}) = 1 - \exp(-h^m(\mathbf{s}, \mathbf{x})) \tag{1}$$

I assume

$$h^m(\mathbf{s}, \mathbf{x}) = \lambda_0 \exp(-\frac{||\mathbf{s} - \mathbf{x}||^2}{2\sigma^2})$$

The independent hazards model is sensible in the case of single camera traps capturing either the left or right flank of individuals. Further, in this case, it is reasonable to assume $h^l(\mathbf{s}, \mathbf{x})) = h^r(\mathbf{s}, \mathbf{x})) \equiv h(\mathbf{s}, \mathbf{x})$ because it is the same physical device capturing one side or the other depending on the orientation of the animal relative to the camera for each visit to the camera trap location. Due to our interest in the single camera trap design I focus on the independent hazards model in the rest of this paper although briefly discuss an alternative model in the next section. The independent hazards model may also be sensible if two distinct

methods are used such as if camera trapping is used in conjunction with localized searching for animal scat (e.g., see Gopalaswamy et al. 2012a) although in this case the devices will not usually be co-located which is unimportant.

Under the independent hazards model, the perfect data, that is if you know identity of individuals, are the *paired* binomial frequencies $\mathbf{y}_{ij} = (y_{ij}^{(l)}, y_{ij}^{(r)})$ for each individual $i$ and trap $j$. This is simply a bivariate version of the standard encounter frequency data which are analyzed by SCR models.

## 2.2 *Multi-state observation model*

In general, the independence assumption may not be reasonable. For such cases a more general model is required that will account for dependence of the devices.

Let $p_i(\mathbf{s}_i, \mathbf{x})$ be the probability of capture for individual $i$ at some trap $\mathbf{x}$ and then, conditional on capture, there are 3 possible encounter states (for sampling by 2 devices): the animal can be captured by device A only, device B only or simultaneously by both devices. Define the conditional encounter probabilities for each possible encounter state by the vector

$$\boldsymbol{\pi}_c = (\pi_A, \pi_B, (1 - \pi_A - \pi_B))$$

and then the unconditional probabilities are

$$\boldsymbol{\pi} = (p_i \pi_A, p_i \pi_B, p_i(1 - \pi_A - \pi_B), 1 - p_i)$$

If the devices are the same type (e.g., both cameras) then we constrain $\pi_A = \pi_B$. This is the case for single camera trap situations and, in that case, the state "captured by both devices" is not possible. In this case the multi-state observation model reduces to the model of the previous section. A sensible parameterization of the cell probabilities for camera trapping with 2 cameras simultaneously would be to define $\pi_{AB}$ as the probability of obtaining photos

of both sides simultaneously and then $(1 - \pi_{AB})/2$ as the probability of obtaining only one side or the other.

Non-independence, such as modeled by the conditional-on-capture multi-state model, will generally result when devices are collocated because encounter in one device should lead to a higher probability of encounter in the 2nd device because the individual is/has already visited the site on that sample occasion.

## 3. Formulation of the model in terms of latent data

For sampling on $K$ sample occasions (usually nights in a camera trapping study) the observed bivariate observation for an individual $i$ of known identity in trap $j$ is $\mathbf{y}_{ij} = (y_{ij}^{(l)}, y_{ij}^{(r)})$, the frequencies of each type of encounter. For single camera studies this is the $2 \times 1$ vector of left and right capture frequencies out of $K$ occasions, and these capture frequencies are binomial outcomes with parameter $p^m(\mathbf{s}, \mathbf{x})$ according to Eq. 1. A key point of the subsequent development of things is that the paired data $\mathbf{y}_{ij} = (y_{ij}^{(l)}, y_{ij}^{(r)})$ are latent when left and right sides cannot be perfectly reconciled. Instead we observe two data sets of left and right flank encounters having arbitrary (unreconciled, or 'scrambled') row order. These two data sets are linked to the perfect data $\mathbf{y}_{ij}$ by a reordering of the rows of one or the other of the data sets. As a simple illustration Table 1 shows a hypothetical data set that could be observed based on 4 traps with coordinates (1,2), (1,1), (2,2), (2,1) respectively and only $K = 1$ sample occasion.

[Table 1 about here.]

These data could represent 7 different individuals or there could be 4 individuals with each row on the right reconciled to one on the left, we can't know without further information. However, if we knew how to match the right encounter histories with the left encounter histories then we can create our perfect data set $\mathbf{y}_{ij}$ being the matched left- and right-

encounter frequencies for each individual. In the sample data given in Table 1, if we knew that the rows were in individual order then the perfect data for individual $i = 1$ (row 1), i.e., the left and right encounters $\mathbf{y}_{1j} = (y_{1j}^{(l)}, y_{1j}^{(r)})$, are $(0, 1)$, $(1, 0)$, $(0, 0)$, and $(0, 0)$ for the 4 traps. The perfect data can only be constructed conditional on the ID of the right-side data. Of course, in practice, we don't know which rows in the right match with rows in the left. Lacking specific information on individuals to make this linkage, one might wonder how it is possible to associate right encounter histories with left encounter histories. The answer is that such information comes from the configuration of traps and encounters of individuals in traps. In our small example, not knowing the true identity of individuals, we observe a left side individual captured in trap 4 and also a right side individual captured in trap 4. It stands to reason that the right side individual is more likely to be the same individual as left side individual 2 than left side individual 1 which was only caught in trap 2. Of course to start making specific probability statements about this we need to be spatially explicit about our model for encounter probability and the distribution of individuals in space. I do this in the next section.

To distinguish the left and right data sets we'll use the notation $\mathbf{Yl}$ and $\mathbf{Yr}$ to be $M \times J$ matrices of encounter frequencies. Under data augmentation these are of the same dimension but the rows of the two observed matrices are not reconciled to individual and therefore do not correspond to the same individual except by random chance. Despite this, I'll retain the use of a single subscript $i$ to index rows. Thus, $\mathbf{Yl}_i = (y_{i1}^{(l)}, y_{i2}^{(l)}, \ldots, y_{iJ}^{(l)})$ and $\mathbf{Yr}_i = (y_{i1}^{(r)}, y_{i2}^{(r)}, \ldots, y_{iJ}^{(r)})$ are the left and right encounter frequencies, respectively, in each trap $j = 1, 2, \ldots, J$. For $K = 1$ these are vectors of binary encounters. If $K > 1$ then elements are binomial frequencies based on a sample size of $K$.

3.1 *Modeling the left-side data set*

To formalize the inference framework I first formulate the problem as an ordinary SCR model for the left-sided encounter histories and define the true identity of each individual in the population to be the row-order of the left-side data set. So in the above example define individuals 1-4 to be the rows of the left side encounter history matrix in whatever arbitrary order they are assembled by the data collector. Note: we could define things vice versa, individuality defined by the right side data set, but it makes sense to define the identity based on the larger of the two data sets so there are fewer unknown IDs to match up (see below). Henceforth I assert that left is always the larger data set. If this is not the case for a particular data set, then we just relabel the data sets.

The appropriate model for the left-side data is a variation of the ordinary SCR model which has been described in a number of places including Borchers and Efford (2008) and Royle et al. (2014, ch. 5). I briefly describe the model here noting that the full likelihood formulation from Royle et al. (2014) is adopted and not the conditional likelihood formulation of Borchers and Efford (2008) although one could formulate the model either way. The left data are the $n_{left} \times J$ matrix of individual and trap specific encounter frequencies (out of $K$ nights of sampling). These are binomial random variables with index $K$ and probability $p(\mathbf{s}_i, \mathbf{x}_j)$ where $\mathbf{x}_j$ is the location of trap $j$ and $\mathbf{s}_i$ is the activity center of individual $i$, a latent variable.

I adopt a Bayesian analysis of this model because that proves convenient in dealing with the unknown identity of the right-side encounter histories. In particular, I use the data augmentation approach to deal with unknown $N$ (Royle et al. 2007, Royle and Young 2008, Royle 2009, Royle and Dorazio 2012) in which the observed encounter history matrix is augmented with a large number of all-zero encounter histories bringing the total size of the data set up to $M$, with $n_{left}$ observed encounter histories (as in the left column of the

Table above) and then $M - n_{left}$ all-zero encounter histories. We also introduce a set of $M$ latent variables $z_i$ which accounts for the zero-inflation of the augmented data set. These data augmentation variables have a Bernoulli distribution with parameter $\psi$. Under data augmentation inference is focused on the parameter $\psi$ instead of population size $N$, but the two are related in the sense that $N \sim \text{Binomial}(M, \psi)$. Finally, to do a Bayesian analysis of the SCR model for the left-side data set we need to introduce the latent activity centers $\mathbf{s}_i$ which are missing data for all $M$ individuals in the augmented data set. All of these details about Bayesian analysis of SCR models using data augmentation are found in Royle et al. (2014) and previously cited papers.

Under the data augmentation formulation of the model, the model for $\mathbf{y}_{ij}$ the latent or ideal data (when identity is known), is specified conditional on the data augmentation variables $z$:

$$y_{ij}^{(l)}|(z_i = 1) \sim \text{Binomial}(K; p(\mathbf{s}_i, \mathbf{x}_j))$$

and

$$\Pr(y_{ij}^{(l)} = 0) = 1 \text{ if } z_i = 0$$

The last expression just states that if $z_i = 0$ then the only possible encounter event is "not captured" which will occur $K$ times at each trap $j = 1, 2, \ldots, J$.

Generalizations of the encounter model are achieved directly by working with the binary encounter events $y_{ijk}$ in which case the basic observation model is Bernoulli instead of binomial (Borchers and Efford 2008; Royle et al. 2014). For example, to model a trap-specific behavioral response we would need to formulate the model in terms of the Bernoulli components instead of the binomial frequencies.

3.2 *Linking the right-side encounter histories with the left-side encounter histories*

Now consider the right-side encounter histories. These individuals are of the same population as the left-side individuals so we will consider that these right-sided individuals must be associated uniquely with the left-sided individuals in the population. As our data sets are augmented to include all-0 encounter histories this means that some right-sided individuals *could* be matched with left-sided individuals that were not captured. Therefore, each right-sided individual which also include $M - n_{right}$ all 0 encounter histories must be uniquely matched to one of the left-sided individuals *and* the pair of data augmentation variable and activity center $(z, \mathbf{s})$ that goes with the left-sided individual. To be clear about this: the $z$ and $\mathbf{s}$ latent variables are associated with the left-sided population. Their 'order' or identity will never change – $z_i$ and $\mathbf{s}_i$ belong with $\mathbf{Yl}_i$, always. However, $\mathbf{Yr}_i$ will *not* be associated with $z_i$, $\mathbf{s}_i$ and $\mathbf{Yl}_i$ in the arbitrary order by which data sets are assembled and so the "labeling" of rows of $\mathbf{Yr}$ is an unknown parameter of the model.

Conceptually we make this linkage by introducing a latent ID variable, $\mathbf{ID} = (ID_1, ID_2, \ldots, ID_M)$ where $ID_i$ is the true identity of right-sided individual $i$. That is, $ID_i$ indicates which left-sided individual right-sided individual $i$ belongs to. Formulated in this way we can develop an MCMC algorithm for this problem that treats the ID variables as latent variables. Conditional on the $ID$ variables then, we reorder the rows of $\mathbf{Yr}$, then recombine $\mathbf{Yl}$ and $\mathbf{Yr}$ into the perfect data set which *is* in individual order. Then, given the perfect data set, we can sample each parameter of the model using standard MCMC methods (Royle et al. 2014, ch. 17). The prior distribution for the ID variables under simple random sampling without replacement of the left-side IDs, from the population of $M$ augmented individuals, is $\Pr(ID_i) = n_{right}/M$, the standard result for sampling without replacement from a finite population, which doesn't depend on the parameters of the model (note that

data augmentation replaces the unknown population size $N$ with the fixed dimension $M$, see

Royle et al. 2007).

Conditional on the vector of ID variables, **ID**, denote the re-ordered right-side data set

by $\mathbf{Yr}^*$ having elements $y_{ij}^{(r*)}$ where now the $i$ subscript is ordered consistent with left-

side observations $y_{ij}^l$. Then the observation model is the same as the left-sided encounter

frequencies:

$$y_{ij}^{(r*)}|(z_i = 1) \sim \text{Binomial}(K; p(\mathbf{s}_i, \mathbf{x}_j))$$

and

$$\Pr(y_{ij}^{(r*)} = 0) = 1 \text{ if } z_i = 0$$

## 4. Estimation by MCMC sampling from the posterior distribution

Essentially the model described above can be regarded as a model for perfect SCR data

where the perfect SCR data are linked deterministically to the observable data, through a

latent ID variable which simply reorders one part (the right-sided encounter histories) of the

data set. As such, to analyze the model by MCMC we need to do MCMC analysis of the

model for the perfect SCR data and then add a Metropolis step to update the ID variables.

An overview of the algorithm is described as follows, and a specific implementation in the

R language is given in the appendix. I don't give much detail here because there is nothing

special about the algorithm – it is plain vanilla Metropolis-Hastings combined with Gibbs

sampling, applied to the basic SCR model.

0. Augment the $\mathbf{Yl}$ and $\mathbf{Yr}$ data sets with all-zero encounter histories to bring them both to

dimension $M \times J$.

1. Initialize all parameters, $p_0$, $\sigma$, $\psi$ for the "single camera trap" model, and the $M$ data

augmentation variables $z_i$ and the $M$ ID variables.

2. Given the current value of the ID variables we simply re-order the rows of **Yr** so they are in individual-order (consistent with the **Yl** data set). We call this re-ordered data set **Yr**$^*$.

3. Given the **Yl** and **Yr**$^*$ data sets, encounter histories we can construct the reconciled individual and trap specific frequencies $\mathbf{y}_{ij} = (y_{ij}^{(l)}, y_{ij}^{(r*)})$.

4. Conditional on the current perfect data set, we can update SCR model parameters $\sigma$ and $p_0$ conditional on the current encounter history configuration using standard Metropolis-Hastings.

5. We update each ID variable that is unknown using a standard Metropolis step. We note that each left-side individual can only have a single right-side individual associated with it. Thus we have to sample IDs without replacement. However, this is conveniently done sequentially, one right-side individual at a time, by swapping ID's between a pair of right-side individuals. That is, for each right-side individual, we pick a different right-side individual, and we *swap* their $ID_i$ values to produce a candidate ID vector **ID**$^*$. Given the candidate ID vector, which is to say the ID vector having made a potential swap, we have to recompute the perfect data set and then the acceptance ratio for the candidate value of $ID_i$ is the likelihood ratio of the perfect data given the candidate value of $ID_i$ to the current value of $ID_i$. We used a distance neighborhood to look for potential IDs to swap and the result is a non-symmetric proposal distribution which must be accounted for by the usual Metropolis acceptance probability. We can cycle through the right-side encounter histories for a set number of swaps (e.g., 10, 50 or 100). Too few doesn't update enough IDs during any MCMC iteration but too many is inefficient because it updates many of the IDs multiple times.

6. We update each $z_i$ variable as in an ordinary SCR model (see Royle et al. 2014, chapt. 17).

7. We update each $\mathbf{s}_i$ as done in an ordinary SCR model (see Royle et al. 2014, chapt. 17).

An R script for simulating data and for fitting the model to simulated data is provided in an R package located at `https://sites.google.com/site/spatialcapturerecapture/misc/1sided`. There are no important technical considerations in implementing this algorithm for the single-flank camera trapping situation. However, it is extremely helpful to choose initial values for $ID_i$ which associate each right-sided individual with a left-sided individual that is not to far away, or else the possibility exists that, for the current (or starting) value of $\sigma$ you could have an encounter that has 0 probability of happening. The R code includes a function that will sort through $ID$ matches to find a set of matches which minimizes the total distance of captures between matched pairs.

### 4.1 *Known identity individuals*

In some studies, even if the study uses only a single camera trap per station, some of the individual ID's may be known. For example, it is common to conduct a telemetry study that is often done simultaneous to a capture-recapture study. The individuals physically captured for telemetry will be known perfectly and thus when they are detected by the capture recapture study their identity will be known. In the MCMC algorithm outlined above, by convention, we organize the left and right data sets so the first $n_{known}$ rows correspond to these "known ID" individuals. In the case of an independent telemetry study which produces the first sample of captured individuals it may be reasonable to assume that the known-ID individuals are selected randomly from the population of $N$ individuals on the state-space $\mathcal{S}$ (Chandler and Royle 2013; Sollmann et al. 2013a) and that the number of known-ID individuals is known perfectly. Under these two assumptions, the encounter observations for the known-ID individuals are regarded as binomial encounter frequencies on par with the individuals observed in the capture-recapture study but they are not used to provide information about $N$. Then, the SCR model provides an estimate of the number of individuals whose true ID

is unknown. Note also that some known-ID individuals may not show up in the capture-recapture study and, in this case, their all-zero encounter history is *observed*.

### 4.2 *The heuristic estimator*

An intuitive procedure for dealing with left- and right-side encounter histories is to treat them as independent samples from the sample population having a single $N$, $p_0$ and $\sigma$ parameter. This is easy to do using the data augmentation approach by introducing 2 sets of latent data augmentation variables say $z_{left,i}$ and $z_{right,i}$ which are independent of one another but have a common Bernoulli($\psi$) distribution. The model in this case is just that of two independent SCR models and the MCMC algorithm described by Royle et al. (2014, ch. 17) applies directly (but duplicating the likelihood part).

We expect that this procedure should yield unbiased estimates of population size and hence density. On the other hand there may be a misspecification of variance because it regards the observed data as two independent data sets of size $n_{left}$ and $n_{right}$, i.e., on average twice the number of individuals you actually observe. In reality there is a non-independence between the encounter histories that the heuristic estimator is not accounting for. In fact, the model allowing for ID to be unknown, described in this paper, accommodates that dependence structure formally and so it *is* the model for non-independence of the left- and right-side encounter histories.

## 5. Analysis of a data set

I simulated a data set with $N = 60$ individuals exposed to trapping by a $5 \times 5$ grid of single camera traps having unit spacing. The arrangement of traps along with trap numbers of identification purposes is shown in Fig. 2. Data were generated using the hazard model having form $p(\mathbf{s}, \mathbf{x}) = 1 - \exp(-h(\mathbf{s}, \mathbf{x}))$ with

$$h(\mathbf{s}, \mathbf{x}) = p_0 \exp(\frac{-||\mathbf{s} - \mathbf{x}||^2}{2\sigma^2})$$

and with $\sigma = 0.5$ and $p_0 = 0.2$. This generated a data set investigated here that has $n_{left} = 28$ left side individuals and $n_{right} = 24$ individuals. Because the data are simulated, it is known that the total number of observed individuals was 30. Posterior summaries based on 1000 burn-in and 2000 post-burn in samples are given in Table 2.

[Table 2 about here.]

We see the posterior of $N$ is not too far from the truth (mean 54), nor are the posterior means of $\sigma$ and $p_0$ far from the data generating values for this specific realized data set.

[Figure 2 about here.]

Let us consider using our posterior simulated results for the $ID$ variable to estimate the identity of individual right-side 11 which was captured 2 times in trap 25 but no other traps. There were a number of individuals in the left data set caught in close proximity to right-side 11 and we're especially interested in whether the model associates right-side individual 11 with these nearby left-side individuals. To investigate this, capture frequencies of the 18 individuals ordered by closeness of average capture location to individual right-side 11 are shown in Table 3. Only the frequency of captures in traps 13-25 are shown as the other traps are distant from trap 25. We see a number of candidates that right-side 11 may belong to. In particular, the left-side individual 16 here was captured 1 time in each of traps 20 and 25, left-side 21 was captured once each in trap 24, and so on. To see how the model evaluates this information the posterior frequency of ID is shown in the column "post. Freq." We see that in fact the posterior ID of individual right-side 1 is highly associated with those left-side individuals captured in its vicinity. Note also that there were 391 posterior samples where right-side 11 is judged to be a "new" individual. That is, *not* one of the 28 captured left-side individuals. In fact, because we simulated the data and know the true identity in this case we know that right-side 11 is actually the same as left-side individual 11 which receives

posterior mass 216/2000 and was captured two times in trap 20 (a neighboring trap). The model seems to be doing a sensible thing in this instance.

[Table 3 about here.]

As a 2nd example, consider right-side individual 21 which was caught 1 time in trap 4. The posterior frequency distribution is shown in Table 4 where the frequencies of encounter in traps 1-12 are shown, because those are closest to the capture of individual 21 in trap 4. Note also that the posterior frequency that right-side individual 21 was *not* associated with any observed left-side individual was 201/2000. In fact, this individual actually belongs with left-side individual 13 and so the model predicts the correct individuality with probability 0.73.

[Table 4 about here.]

We can match up individuals like this all day and it's a lot of fun to see the model decide which individuals captured on the right-side should be matched to left-side individuals. It's almost more fun than the objective of estimating population size.

## 6. Simulation study

To evaluate the performance of the SCR model of single-sided camera trapping, I did a simulation study focused on estimating population size $N$ using a $5 \times 5$ grid of traps having unit spacing. The state-space for the SCR model was constructed by buffering the square trap array by 2 units. Parameter values were structured according to a factorial design with 2 levels of $N$ (80,120) two levels of $\sigma$ (0.70, 0.50) and 2 levels of $p_0$ (0.20, 0.10), for a total of 8 distinct scenarios. For each of the 8 parameter settings I evaluated 4 estimation scenarios: (1) A perfect data situation in which the true ID is known for all individuals so that left and right side encounter histories can be reconciled perfectly; (2) 10 individuals have known ID such as captured for telemetry prior to the capture-recapture study. Thus, the right and

left side of these 10 individuals is reconciled perfectly; (3) none of the right-side individuals have a known ID and therefore ID must be determined using the model described in this paper; and (4) the heuristic estimator as described in section 4.2. Thus, a total of 32 distinct estimation scenarios were carried out (8 parameter scenarios times 4 estimation scenarios). The first estimation scenario is an ordinary capture-recapture model but with left- and right- photos recorded separately and, as a result, maybe occur with unequal frequency by chance. This is not a typical data structure although such data could easily be recorded in practice. Here it serves to provide a baseline to which the remaining cases, which have relatively less information, can be compared. Two-hundred (200) data sets were simulated for each of the 32 parameter/estimation scenarios and analyzed by MCMC by sampling 21000 values from the posterior distribution, discarding the first 1000 values as burn-in. Each MCMC analysis took between 1 and 2 hours of CPU time, thus about 200-400 CPU hours for each of the 32 scenarios. Summaries of the posterior distribution were computed for each of the 200 simulated data sets, including the posterior mean and posterior mode. A frequentist evaluation of the 'sampling error' was computed as the standard deviation among the posterior summaries for the 200 data sets. In addition I computed the frequentist coverage of a 95% confidence interval for $N$ based on the 2.5 and 97.5 percentiles. Finally I computed the average posterior standard deviation and the expected posterior mode by pooling the posterior distributions from all 200 data sets.

The values of the parameters were chosen by trial-and-error to produce data sets of variable expected sample sizes of captured individuals. See Table 5 for the average sample sizes of total number individuals and total capture events. The high value of $N$ should generate high sample sizes of individuals and, as a result, more uncertainty in individual assignment as there will be more individuals in the vicinity of each trap. Thus we expect relatively better performance in the $N = 80$ scenarios, which is to say more loss in precision compared to

"all known" and relatively better precision compared to the heuristic estimator. Similarly if we were to increase the number of traps, holding $N$ constant, we should expect improved performance (see Chandler and Royle 2013 for a similar phenomenon). Simulation results for the $N = 120$ cases are summarized in Table 6 (the $N = 80$ cases are given in the Appendix).

[Table 5 about here.]

[Table 6 about here.]

Some salient points of the results presented in Table 6 are summarized here: 1. Main interest is in the basic estimator when we have no known ID individuals. That is, the $nID = 0$ case. For this case we see the posterior mode is usually centered over the correct value (120, 120, 120, 119) for the 4 cases. The average posterior mean, if used as a frequentist point estimator, indicates small bias due to the slight skew of the posterior distribution. The average coverage of 95% posterior intervals is about 94%. The posterior SD for this case is usually ¡ 10% larger compared to the "all known" case. However, for the $\sigma = 0.5$, $p_0 = .10$ case (relatively sparse in terms of recaptures) we see that the posterior SD is about 20% worse than the known ID case. 2. As the information content increases from 0 known to 10 known to all known we naturally see an increase in precision of the posterior mean and mode as frequentist point estimators, and a decrease in average posterior SD. 3. The heuristic estimator performs only slightly better than the "0 known" case in terms of frequentist SD of the mean and mode as point estimators. The coverage of a 95% confidence interval is only about 90% when averaged over the 4 cases. The estimator is too liberal which may be an expected result due to the heuristic estimator over-counting the sample size (treating left and right side data sets as two independent data sets). This shows up in the smaller posterior standard deviations for the heuristic estimator.

## 7. Discussion

I developed a spatial capture-recapture model for dealing with individual encounter history data in which individuality is imperfectly observed. The specific motivating example is camera trapping using a single camera trap. In such cases, only left or right side photos are obtained, and there is no direct information about which right-side encounter history goes with which left-side encounter history. Even when 2 camera traps are used at each site (or a subset of sites) sometimes only one flank of the animal will be identifiable either due to poor image quality or failure of the device. In practice these one-sided cases have been ignored unless a subsequent match is produced from 2 simultaneous images. Thus the model I proposed here allows for more data to be used from standard 2-camera trap studies and it also allows for the flexibility of 1-camera per site studies.

The basic model of uncertain identification is similar to Link et al. (2010) and indeed the Link et al. (2010) idea was applied by Bonner and Holmberg (2013) for multiple sampling methods and McClintock et al. (2013) to the problem of bilateral photo identification. However the model I described here is distinct in that it is *spatially explicit* so that it accommodates the spatial arrangement of capture events which are in fact highly informative about individuality. Previous other treatments of uncertain identity in capture-recapture models (Wright et al. 2009, Link et al. 2010, etc..) ignored spatial information that is inherent in essentially all capture-recapture studies, especially camera trapping studies. Intuitively, and as I showed in the example, the configuration of encounters strongly affects the posterior probabilities of individual association. Chandler and Royle (2013) also deal with a type of SCR model that accommodates uncertain ID. In their model they assume that individual detections are not identifiable to individual (or a subset is perfectly identifiable) and they formulate the model in terms of a completely latent set of $N$ encounter histories. In the present problem, we can construct either left-side or right-side encounter histories but are

unable to link the two data sets. The sample-based uncertainty as in Chandler and Royle (2013), instead of individual-based uncertainty considered here, may be accommodated in the present model which will be elaborated on in the sequel.

Simulation results show that the model which accommodates unknown ID typically performs well in terms of posterior mode (being centered near the data generating value), and has small frequentist bias and near the nominal 95% frequentist interval coverage. In all cases of the proposed estimator considered, the overall posterior mode was within 1 individual of the true population size, indicating that the posterior is centered over the data-generating value. Results showed that there are increases in frequentist and posterior precision as the number of known ID individuals increases (from 0 to 10 to 'all'). Compared to the heuristic estimator, which falsely assumes left and right side data sets are independent samples of the population, the model which accommodates unknown ID typically out-performs slightly in terms of frequentist standard deviation of the posterior mean and mode. The heuristic estimator is too liberal, under-states posterior standard deviation, and produces confidence intervals with less than nominal 95% coverage. This is to be expected since the heuristic estimator over-states the sample size, counting left-side and right-side encounter individuals as independent data sets.

The model proposed here accommodates the spatial arrangement of samplers but does not require that the two sampling methods be co-located (for an example see Gopalaswamy et al. 2012a). Whether samplers are co-located or not changes the possible observation states only. For example, if single camera traps are used and DNA sampling based on quadrat searches for scat are the 2nd method, and the coordinates are not coincident, then $p^{camera} = 0$ for camera trapping at the DNA sites and $p^{DNA} = 0$ for DNA at the camera trapping sites.

The model proposed here seems to have direct relevance to the case of DNA sampling when there are partial genotypes. For example, if a sample has 8 out of 10 loci determined,

with 2 missing, then the true genotype should be regarded as latent and the model proposed here, with some modifications, will integrate the spatial encounter information with data on the observed loci, to give a probabilist match with available genotypes in the vicinity (including possibly new genotypes in the augmented population). A related problem is that of genotyping error where, for any particular locus, there is some probability that the observed allele is in error. This problem is particularly interesting because genotyping error has received considerable attention recently (Lukacs and Burnham 2005; Wright et al. 2009) but, as in our motivating camera trapping problem here, the spatial information about individuality has not previously been incorporated into existing methods that deal with genotyping error. As in camera trapping, when individuality is obtained from DNA sampling such as from hair snares or scat obtained by dog searches, the spatial location of captures should also be informative about individuality. Thus, the basic idea developed here should be relevant to genotyping uncertainty and also dealing with partial genotypes.

**Acknowledgments**

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**Figure 1.** Female wolverine, Southeast Alaska, being simultaneously photographed and it's hair sampled by an alligator clip set-up (photo credit: A. Magoun, taken from Magoun et al. 2011a). Wolverines can be uniquely identified by the bib pattern on their chest (Magoun et al. 2011b).
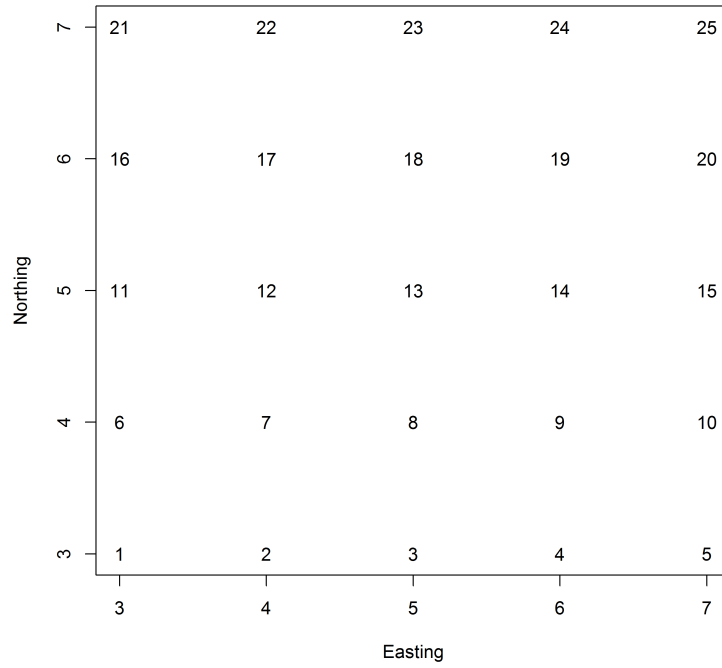
**Figure 2.** Grid of 25 traps of unit spacing used in simulating left-sided and right-sided encounter history data from a study using a single camera-trap per site. Trap identifier is given for reference in text.

**Table 1**
*A typical encounter history data set constructed from left and right-sided photos with no ability to reconcile the two. For each data set the rows index individual but not across data sets.*

| trap | Left data set | | | | Right data set | | | |
|------|---|---|---|---|---|---|---|---|
|      | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
|      | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
|      | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
|      | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
|      | 0 | 0 | 0 | 1 |   |   |   |   |

**Table 2**

*Posterior summaries of model parameters from a simulated population of $N = 60$ individuals, $p_0 = 0.20$ and $\sigma = 0.50$. The population was augmented to $M = 120$ individuals and therefore $\psi = 0.50$.*

| parameter | mean | SD | 2.5% | 25% | 50% | 75% | 97.5% |
|-----------|------|-----|------|-----|-----|-----|-------|
| $p_0$ | 0.182 | 0.033 | 0.126 | 0.160 | 0.177 | 0.204 | 0.254 |
| $\sigma$ | 0.517 | 0.037 | 0.450 | 0.487 | 0.517 | 0.543 | 0.590 |
| $\psi$ | 0.452 | 0.080 | 0.313 | 0.394 | 0.448 | 0.505 | 0.619 |
| $N$ | 54.006 | 8.101 | 41.000 | 48.000 | 53.000 | 59.000 | 72.000 |

**Table 3**

*Posterior assignment of right-side individual 11, captured twice in trap 25, to various left-side individuals. The posterior frequency of an ID match is shown in the far right column. For example, 692 posterior samples show that right-side individual 11 goes with left-side individual 16. The true ID in this case has right-side 11 also belonging to left-side 11 (note: right and left IDs are arbitrary so this is a coincidence). The middle columns of the table are trap identifications and the numbers are frequency of capture in each trap.*

| leftID | Trap ID | | | | | | | | | | | | | post. Freq. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | |
| 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 692 |
| 7 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 72 |
| **11** | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 216 |
| 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 288 |
| 22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 342 |
| 24 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 27 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| 15 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 |
| 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 17 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 19 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 391 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 391 |

**Table 4**

*Posterior assignment of right-side individual 21, caught 1 time in trap 4, to eighteen other individuals captured in close proximity. The posterior frequency of an ID match is shown in the far right column. For example, 1469 posterior samples show that right-side individual 21 goes with left-side individual 13 which is the true ID of right-side individual 21. The middle columns of the table are trap identifications and the numbers are frequency of capture in each trap.*

| leftID | Trap ID | | | | | | | | | | | | post. Freq. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | |
| **13** | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1469 |
| 26 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 326 |
| 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 5 |
| 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 |
| 5 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 27 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 14 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 28 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| none | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 201 |

**Table 5**

*Expected number of unique individuals captured ($n_{left}$, $n_{right}$) and total number of capture events ('caps') for each simulation scenario. Three table sections represent no known ID individuals ($nID = 0$), 10 known ID individuals ($nID = 10$) and all known ($nID = all$). Note that in the first two groups where individuals have unknown ID the data sets are ordered upon collection so that the left-side encounter history data set is larger, so you see a systematically larger left-side data set.*

no known ID individuals, $nID = 0$

| | | N=120 | | | | N=80 | | | |
|---|---|---|---|---|---|---|---|---|---|
| $p_0$ | $\sigma$ | $E(n_{left})$ | caps | $E(n_{right})$ | caps | $E(n_{left})$ | caps | $E(n_{right})$ | caps |
| 0.20 | 0.70 | 79.2 | 278.5 | 75.6 | 273.9 | 53.1 | 184.7 | 50.4 | 181.0 |
| 0.10 | 0.70 | 65.4 | 143.3 | 61.4 | 137.3 | 44.3 | 96.3 | 41.1 | 91.1 |
| 0.20 | 0.50 | 58.8 | 142.9 | 55.5 | 137.4 | 40.0 | 96.1 | 37.4 | 90.8 |
| 0.10 | 0.50 | 45.8 | 74.3 | 41.8 | 68.5 | 31.8 | 50.9 | 28.8 | 46.0 |

10 known ID individuals, $nID = 10$

| | | N=120 | | | | N=80 | | | |
|---|---|---|---|---|---|---|---|---|---|
| $p_0$ | $\sigma$ | $E(n_{left})$ | caps | $E(n_{right})$ | caps | $E(n_{left})$ | caps | $E(n_{right})$ | caps |
| 0.20 | 0.70 | 82.0 | 278.5 | 78.4 | 273.9 | 55.9 | 184.7 | 53.2 | 181.0 |
| 0.10 | 0.70 | 69.2 | 143.3 | 65.1 | 137.3 | 48.1 | 96.3 | 44.8 | 91.1 |
| 0.20 | 0.50 | 63.4 | 142.9 | 60.1 | 137.4 | 44.6 | 96.1 | 42.0 | 90.8 |
| 0.10 | 0.50 | 51.1 | 74.3 | 47.2 | 68.5 | 37.0 | 50.9 | 34.1 | 46.0 |

all known ID individuals, $nID = all$

| | | N=120 | | | | N=80 | | | |
|---|---|---|---|---|---|---|---|---|---|
| $p_0$ | $\sigma$ | $E(n_{left})$ | caps | $E(n_{right})$ | caps | $E(n_{left})$ | caps | $E(n_{right})$ | caps |
| 0.20 | 0.70 | 87.3 | 278.4 | 87.3 | 271.4 | 58.3 | 185.2 | 58.3 | 180.5 |
| 0.10 | 0.70 | 76.0 | 145.7 | 76.0 | 137.9 | 50.6 | 97.0 | 50.6 | 90.7 |
| 0.20 | 0.50 | 65.3 | 142.7 | 65.3 | 136.4 | 43.9 | 96.7 | 43.9 | 91.0 |
| 0.10 | 0.50 | 56.2 | 74.8 | 56.2 | 69.0 | 36.6 | 49.4 | 36.6 | 44.2 |

**Table 6**

*Simulation results for the population size parameter N under the N = 120 scenarios. For each of the parameter settings (cases 1-4), four different estimators are considered: 'nID=0' is that in which no individuals have known ID, 'nID=10' and 'nID=all' are 10 known and all known, respectively, and 'heur' is the heuristic estimator which regards left and right side encounter histories as independent samples from the posterior distribution. For each case (organized in rows), summaries are the mean of the posterior mean and mode over 200 simulated data sets ('mean' and 'mode' respectively) and the standard deviation of those 200 values ('sd'), the average posterior standard deviation ('postSD'), the frequentist coverage of a 95% posterior interval based on the 2.5 and 97.5 percentiles ('95cover') and the overall posterior mode ('pmode').*

Case 1: $\sigma = 0.7, p_0 = 0.20$

| Model | mean | sd | mode | sd | postSD | 95cover | pmode |
|---|---|---|---|---|---|---|---|
| nID=0 | 120.076 | 8.248 | 118.970 | 8.335 | 7.772 | 0.935 | 120 |
| nID=10 | 120.064 | 7.847 | 118.953 | 7.872 | 7.405 | 0.950 | 119 |
| nID=all | 120.851 | 7.345 | 119.698 | 7.357 | 7.223 | 0.915 | 120 |
| heur | 120.73 | 8.063 | 120.027 | 8.183 | 6.499 | 0.850 | 119 |

Case 2: $\sigma = 0.7, p_0 = 0.10$

| Model | mean | sd | mode | sd | postSD | 95cover | pmode |
|---|---|---|---|---|---|---|---|
| nID=0 | 121.844 | 10.491 | 120.235 | 10.354 | 10.314 | 0.930 | 120 |
| nID=10 | 121.778 | 10.086 | 120.33 | 10.203 | 9.771 | 0.925 | 120 |
| nID=all | 120.866 | 8.931 | 119.562 | 9.008 | 9.228 | 0.940 | 119 |
| heur | 120.768 | 10.269 | 119.534 | 10.264 | 8.976 | 0.915 | 117.5 |

Case 3: $\sigma = 0.5, p_0 = 0.20$

| Model | mean | sd | mode | sd | postSD | 95cover | pmode |
|---|---|---|---|---|---|---|---|
| nID=0 | 121.250 | 11.545 | 119.780 | 11.481 | 11.114 | 0.930 | 120 |
| nID=10 | 121.010 | 10.707 | 119.275 | 10.597 | 10.569 | 0.920 | 120 |
| nID=all | 121.980 | 10.094 | 120.435 | 9.838 | 10.493 | 0.960 | 122 |
| heur | 122.276 | 10.823 | 121.188 | 10.662 | 9.135 | 0.890 | 120.5 |

Case 4: $\sigma = 0.5, p_0 = 0.10$

| Model | mean | sd | mode | sd | postSD | 95cover | pmode |
|---|---|---|---|---|---|---|---|
| nID=0 | 123.736 | 15.049 | 120.799 | 15.120 | 15.572 | 0.955 | 119 |
| nID=10 | 124.041 | 14.566 | 121.135 | 14.599 | 14.737 | 0.955 | 122 |
| nID=all | 121.507 | 13.368 | 119.412 | 13.363 | 12.985 | 0.935 | 118 |
| heur | 121.906 | 14.783 | 119.201 | 14.708 | 14.117 | 0.935 | 117.5 |